PECULIARITIES OF DIURNAL VERTICAL MIGRATIONS OF ZOOPLANKTON IN POLAR SEAS[1]

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Studies of diurnal vertical migration in the polar seas are of special interest since we are able to make observations in nature (without the possible drawbacks of laboratory experiments) of the behavior of animals under the widely varying light conditions that prevail during different seasons. Thus, during the polar summer it is possible to investigate the diurnal migration under conditions of uninterrupted daylight, during the polar autumn and spring under changing conditions of alternating days and nights, and finally in winter under conditions of permanent darkness. At present a series of special diurnal stations are available, taken mainly in the Barents Sea, as well as in the White Sea. Unfortunately, owing to weather conditions, no diurnal stations have been obtained as yet in winter and spring.

I. VERTICAL MIGRATIONS OF ZOOPLANKTON UNDER CONDITIONS OF PERMANENT DAYLIGHT (IN SUMMER)

We have a series of diurnal stations taken in the Barents Sea (Bogorov, 1938) and the White Sea (Bogorov, 1941) in summer, as well as unpublished data. The organisms investigated were: *Calanus finmarchicus*, *Pseudocalanus elongatus*, *Microcalanus pygmaeus*, *Metridia longa*, *Metridia lucens*, *Acartia longiremis*, *Oithona similis*, *Harpacticus superflexus*, *Sagitta elegans*, *Oikopleura vanhöffeni*, and larvae of bottom animals; the investigations included adults as well as young stages of development.

The results showed that all the dominant species perform no such regular shiftings during a 24-hour period as are characteristic of more southern latitudes (Esterly, 1911, 1912; Russell, 1925–26–27; Clarke, 1933, 1936, *et al.*). It is known, due to the general occurrence of this phenomenon, that the diurnal vertical migration of plankton is considered one of the essential manifestations of the life activity of plankton affecting the whole biological regime of the sea, both predators and prey (Bogorov, 1939a, b).

[1] Proofs not seen by author.

Even such species as *Calanus finmarchicus* and *Sagitta elegans*, under conditions of diurnal daylight in the Barents Sea in summer, maintain an almost unchanged vertical distribution through the 24-hour period. As already stated (Bogorov, 1938), this almost invariable diurnal vertical distribution is not achieved passively with the organisms merely remaining in the water level selected, but rather it is achieved by active swimming, since the tidal phenomena in the open sea (Zubov, 1932) cause considerable shifting of water particles up and down, which water movement has to be overcome by the organisms. Thus, in the Barents Sea during summer, under conditions of permanent daylight, a) the organisms tend to occupy a definite habitat level with optimum illumination, and b) tidal phenomena force the animals to move constantly upwards and downwards in order to overcome displacement by the movement of water particles and to maintain their habitat level.

The study of this phenomenon in the more southern White Sea is of particular interest. Here, although the surface of the sea is permanently illuminated in summer, the sun lies low on the horizon during the night, so that conditions of light penetration into the water are less favorable and the period of feeble water illumination lengthened.

Investigations of a series of organisms showed that most species maintain an almost constant vertical distribution during the 24 hours. In the White Sea, in the region investigated, only the surface layer is considerably affected by tidal phenomena. Therefore, only the inhabitants of this layer have to perform diurnal vertical migrations of the polar type (such as in the Barents Sea), whereas animals living in deep water layers need no extensive, active migrations to maintain their optimum habitat level.

In contrast with the Barents Sea, in the White Sea the usual type of diurnal vertical migration of plankton also was observed. Thus, for instance, *Metridia longa* is to be found in the surface layers in greater quantities in the evening and night hours than in the daytime. Furthermore, although the vertical distribution of the total quantity of plankton does not vary considerably during the 24 hours, the quantity found in the upper layer is greater in the evening and night than in the morning and afternoon. Therefore, we are here in the presence of a diurnal vertical migration of plankton of the usual (southern) type. Although of not such large magnitude as in more southern seas, its occurrence in the White Sea in the summer emphasizes once more the role of light in the phenomenon of diurnal migration.

II. THE VERTICAL MIGRATION OF ZOOPLANKTON UNDER CONDITIONS OF ALTERNATING DAY AND NIGHT (IN AUTUMN)

What is the behavior of organisms during the period of alternating day and night? If they perform regular diurnal migrations of the usual type during this period, then the role of light in this phenomenon becomes still more evident.

During our observations of the variations in the quantity of zooplankton in the surface layers of the Kara Sea (Table I) in 1934, we

TABLE I. Biomass of Surface Zooplankton and Number of Organisms of Some Species (per 1 m³) in Night and Day hauls Taken in the Southeastern Barents Sea and Western Kara Sea in September, 1940

	Biomass of zooplankton per 1 m³ (in mgs)	*Calanus finmarchicus*	*Pseudocalanus elongatus*	*Acartia*	*Oithona*
Night	200	45	450	210	1500
Day	115	5	370	660	4500

	Temora	*Microcalanus*	*Appendicularia*	Eupheusidae[2]	Polychaeta	Trochophora
Night	410	3100	170	1	74	60
Day	30	2400	2	—	10	1

found that the biomass of zooplankton was greater in the evening and night hauls than in the day hauls. This was due to the fact that several species (*Calanus finmarchicus*, *Fritillaria borealis*, Polychaeta juv., Euphausiidae, and others) occurred chiefly in night hauls. So this is undoubtedly evidence of diurnal vertical migration.

Chmysnikova (1937), in working out the zooplankton material collected in Vilkitsky Strait in September, observed that several species (*Calanus finmarchicus*, *Pseudocalanus elongatus*, *Fritillaria borealis*, and *Sagitta elegans*) occur more often in night hauls than in day hauls. In spite of the fact that this material was not collected on special stations, and moreover, was not treated by any precise quantitative method, the results obtained by Chmysnikova convincingly confirm the occurrence of a diurnal vertical migration of polar zooplankton during the period of alternating day and night.

To obtain a final solution of this problem, we worked out the special four diurnal stations taken in the Barents Sea in October, which was quite an achievement considering the weather conditions prevalent in autumn. As a result, it was established that almost all dominant species perform regular diurnal vertical migrations. During the

[2] The author's spelling is given here, although it is possible that he intended Euphausiidae. Editor.

night great masses of plankton concentrate in the upper layers, whereas in the daytime they sink into the deep waters. This is well illustrated by station no. 4687.

A. The dominant species found on this diurnal station were:

1. *Calanus finmarchicus* st. IV, V, and VI
2. *Metridia longa* st. IV, V, and VI
3. *Metridia lucens* st. IV, V, and VI
4. *Microcalanus pusillus* st. VI
5. *Pseudocalanus elongatus* st. IV, V, and VI.

These undertake regular diurnal migrations in the Barents Sea under conditions of polar autumn, with alternating day and night. Each of these species has its peculiarities, but common to all of them is their aggregation in huge quantities in the upper layer 50–0 m. (Table II),

TABLE II. Percentage Distribution of Organisms of the Dominant Species at Station 4687. Hauls Taken During the 24 Hours Are Divided into Two Periods: Dark, from 6 P. M. to 5 A. M., and Light, from 6 A. M. to 6 P. M. Moreover, All the Hauls Are Grouped into Surface (50–0 m.) and Deep (200–50 m.) Water

Stages	Depth (m.)	*Calanus finmarchicus*		*Metridia longa*		*Metridia lucens*		*Pseudocalanus elongatus*	
		6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m
IV	50–0	63	4	43	12	80	1	39	10
	200–50	37	96	57	88	20	99	61	90
V	50–0	77	1	29	25	85	2	45	6
	200–50	23	99	71	75	15	98	55	94
VI ♀	50–0	92	—	36	—	95	2	73	21
	200–50	8	100	64	100	5	98	27	79

All Stages	Depth (m.)	*Microcalanus pygmaeus*		*Acartia longiremis*		*Oithona similis*		*Oithona plumifera*	
		6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.	6 p. m. to 5 a. m.	6 a. m. to 6 p. m.
	50–0	78	25	70	20	86	80	23	40
	200–50	22	75	30	80	20	20	77	60

often even in the layer 10–0 m. in the hours of darkness. In the daytime, on the contrary, the bulk of the organisms remain in the deep water layers, some of the species descending in the deepest layers of 200–100 and 150–100 m.

A. Not only is the limited diurnal vertical migration characteristic of adults and older stages of development but also of the younger stages of the species mentioned. However, as young stages are scarce at this time of the year they cannot be discussed in detail.

B. Some representatives of the krill always occur in samples in single specimens (a drawback of Nansen's net); however, they are found more often in the upper layers in the hours of darkness and in deep water layers in the daytime.

C. Two dominant species, *Oithona similis* and *O. plumifera*, perform no diurnal vertical migrations even under conditions of alternating day and night.

D. Consequently, the diurnal vertical migrations of plankton in the Barents Sea, under conditions of alternating day and night, are similar to such migrations in all southern seas where this phenomenon, due to its general occurrence, affects the biology (especially the vertical distribution during the 24 hours) of herring and other plankton-eating fishes.

The diurnal migrations of plankton here described are not related to the vertical shifting of water particles during the 24 hours. Hydrographic data show that at these stations the shifting of water particles is very limited, if there is any shifting at all. At different moments of the 24-hour period the temperature distribution at different levels (horizons) remains almost unchanged.

Finally, we may describe the scheme of diurnal vertical migration of zooplankton at different latitudes as follows (Fig. 10).

1. In seas of moderate and southern latitudes, with a permanent regular alternation of day and night, the diurnal migration is of the usual, universal type (Fig. 10B); *i. e.*, once during the 24 hours, with the beginning of twilight, the migrating animals swim upwards, ascending from great depths (often as deep as 500 m.) to the upper layers. At dawn they begin to swim downwards, sinking in the daytime into the deep water layers. During these migrations, which exceed even ½ km., the animals swim through water layers which have quite different physical conditions, seeking in the daytime to avoid unfavorable light conditions, and, in the evening, to reach the upper layers rich in food.

2. In polar seas the diurnal vertical migration is subject to great seasonal changes. Thus in summer (Fig. 10A), under conditions of permanent daylight, the animals maintain an almost invariable vertical distribution, actively or passively (depending on the behavior of water particles) keeping to their habitat level. Since the water particles, under the influence of tidal phenomena, shift twice upwards and twice downwards during the 24-hour period, the animals which remain all the time in one horizon are subject to quite different physico-chemical conditions. They submit to these changes in order to maintain themselves at the level with optimum light conditions.

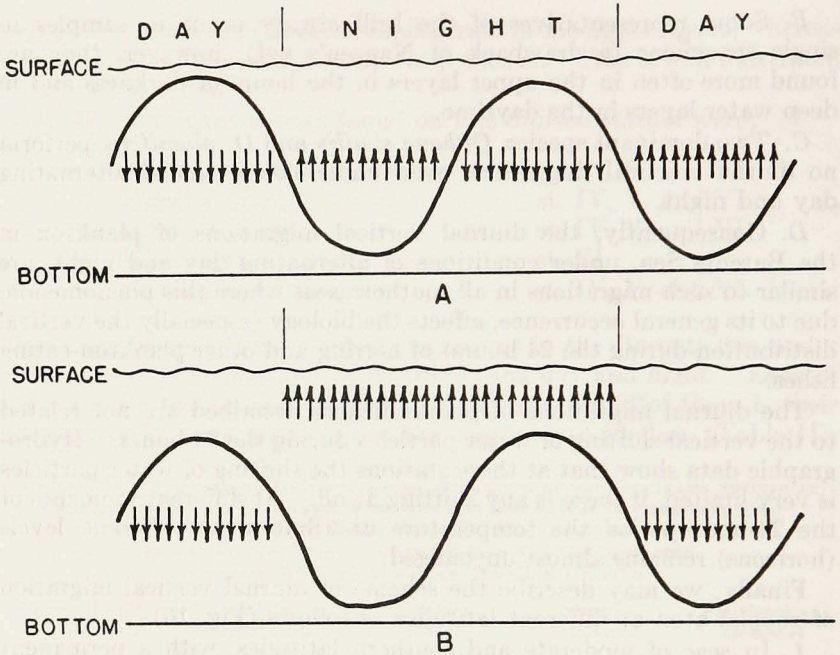

Figure 10. Diagrammatic patterns of diurnal vertical migration under Polar conditions (A) in summer during 24 hours of daylight, and (B) in autumn under conditions of alternating nights and days.

In the more southern White Sea some species exhibit a diurnal vertical migration of the usual type, while others have a more constant distribution which is typical of polar seas. This is explained by the fact that the White Sea is a transition zone in which, although daylight is permanent in summer, the sun lies so near the horizon at night that almost no rays penetrate into the water.

3. In the autumn in the polar seas the days alternate with nights. As a result, the same species and possibly even the same organisms which maintained an invariable vertical distribution during the 24 hours of summer daylight begin to perform migrations of the usual type (Fig. 10B). They swim towards the surface in the dark and downwards in the daytime, passing through water layers with quite different conditions. These data give conclusive evidence of the role of light in the phenomenon of diurnal migration and the importance of this factor for the vertical distribution of plankton.

4. Consequently, the study of the vertical distribution of plankton has a general bearing. It is impossible to assign any species or any age-group to a definite water layer or to definite physico-chemical

conditions without a knowledge of the diurnal vertical migration of the particular group. Since diurnal vertical migrations are characteristic of most zooplankton species (Clarke, 1933, 1934a, b; Gardiner, 1933; Esterly, 1911: Russell, 1927; Rose, 1925, *et al.*), this being a phenomenon of normal life activity during their partial or entire individual life, we can judge the ecological conditions characteristic of a given species only in the light of the phenomenon of vertical plankton migrations. Thus we have to consider all the water layers in which the organisms dwell during the 24 hours as forming the ecological conditions characteristic of the given species.

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